The Fauna of Australian Seagrass Beds

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Australia has a rich seagrass flora (26 species), widely distributed in estuaries and shallow coastal embayments. The fauna of the seagrass beds is diverse and consists of infaunal, epifaunal, epiphytic and epibenthic species. This community is composed of temporary and permanent residents exhibiting tidal, diurnal and seasonal fluctuations. The literature dealing with the fauna of Australian seagrass beds is reviewed and possible food-web relationships and energy flows within seagrass communities are postulated.

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INTRODUCTION

Seagrass beds occur in estuaries and shallow coastal embayments throughout mainland Australia (Larkum, 1976a). In many estuaries they form extensive beds. In eastern temperate Australia, seagrass beds often occur with mangrove and salt marsh communities which together constitute .coastal wetlands (Hutchings and Recher, 1974; AMSA, 1977). In tropical regions this relationship rarely occurs. Instead, seagrass beds may be associated with coral reefs.

Recently in the Caribbean, Ogden and Zieman (1977) have shown the close relationship between coral reefs and seagrasses. Herbivorous coral reef fish migrate from the reef to nearby beds of *Thalassia testudinum* (Banks ex König) to feed. Carnivorous fish and grazing sea urchins move at night from the reef to the seagrass beds to feed. Such migrations have not been documented in Australia.

The role of seagrass beds in estuaries and shallow coastal embayments has become apparent during the past decade in Australia. Seagrass beds provide important habitats for juvenile stages of commercial fish species (Bell *et al.*, 1978a, b) and prawns (Young, 1978), They stabilize and trap sediments improving water clarity (Orth, 1977). A rich fauna is associated with the beds. There are few herbivores of Australian seagrasses and seagrass beds also produce large amounts of organic matter which is then broken down by the fauna of seagrass beds to detritus on which estuarine food chains are dependent (Kirkman and Reid, 1979).

Overseas, considerable information on the fauna of seagrass beds exists. An overview of seagrass faunas throughout the world is provided by Kikuchi and Pérès (1976). They describe the fauna of each region, and then attempt to assess the importance of seagrasses in providing a structural habitat, shelter and a food resource. Food web relationships and energy flows in the seagrass ecosystems are discussed. Other studies have concentrated on regional seagrass communities (Orth, 1973, 1977; Heck, 1977, 1979). Heck studied in detail the epibenthic invertebrates of *Thalassia* beds in Panama. Considerable seasonal fluctuations in both species number and abundance occurred. Sites varied in species composition and abundance and Heck attributed this to the proximity of surrounding habitats especially coral reefs which

contain a number of species that utilize the seagrass meadows. Other workers like Nelson (1979) have studied in detail one faunal component, such as the amphipods.

Other workers have experimentally manipulated seagrass beds to assess the value of habitat complexity in determining species richness and abundance (Heck and Wetstone, 1977). Young and Young (1977, 1978) have studied the effects of predation at various times of the year by caging, adding dense populations of suspension feeders and providing organic enrichment.

Breakdown of seagrass into detritus has been investigated by Robertson and Mann (1980). Isopods and amphipods are important in shredding the intact dead seagrass leaves. The decomposition of organic detritus has been extensively reviewed by Fenchel (1977). Utilization of this detritus and export of this productivity out of the seagrass beds has been considered by Ogden and Zieman (1977; Ogden, 1976) who have studied fish feeding in Caribbean seagrass beds.

OBJECTIVES OF THE REVIEW

To collate and synthesize all the available information on Australian seagrass faunas. This will reveal the dominant species whose life histories and trophic status merit detailed investigations. Such information is essential for estimates of secondary productivity to be made for although it is widely recognized that Australian seagrass beds are important, this is largely based on inference from overseas data. Data on secondary productivity of Australian seagrass beds are non-existent.

From overseas data and limited Australian data there are sound financial and ecological reasons for maintaining seagrass beds (Larkum, 1981). Maintenance requires management but we lack the necessary information for implementation. Instead, as the use of estuaries increases (Burnley, 1974), seagrass beds are being degraded. Larkum (1976b) has shown that the seagrass beds on the northern shores of Botany Bay, New South Wales, have disappeared because of pollution from Cooks River. Seagrass beds on the southern shores of Botany Bay are affected by increased wave action and decreased water clarity caused by dredging associated with the port development. Similar port and industrial developments in Cockburn Sound, Western Australia, have also caused widescale disappearance of seagrass beds during the 1970s and this is well documented by Cambridge (1979).

As estuarine resources are limited in Australia it may be necessary to sacrifice some seagrass beds to keep others. This necessitates the ranking of beds in terms of ecological importance. This can only be done if detailed information exists on a variety of seagrass communities in differing environments.

Finally, it is hoped that this review will reveal the major gaps in our knowledge and stimulate further research.

FLORISTICS OF SEAGRASSES

Seagrasses are angiosperms which are able to live permanently in seawater. Not only are they able to fulfil their normal metabolic activities when fully submerged in seawater but can also complete their generative cycle. All seagrasses have in common a well developed anchoring system. In addition, they can compete successfully with primarily marine organisms such as algae. This combination of properties is so rare among angiosperms that only fifty two species of seagrass have been described (den Hartog, 1970, 1979). Other species are currently being described (Larkum, pers. comm.). Twenty six of these species occur in Australia (Larkum, 1976a). Since 1976 three new species have been described *Posidonia sinuosa,* Cambridge and Kuo, *P.*

augustifolia, Cambridge and Kuo, and *Halophila tricestata,* Greenway. Larkum suggests that latitude 25°S on the west coast and 30°S on the east coast of Australia form a boundary between temperate and tropical species. South of these latitudes the most successful community is formed by *Posidonia australis* Hook f. This species forms extensive monospecific beds in sheltered conditions. In New South Wales and Western Australia the beds rarely extend below -10m (depth below mean low water mark), but in the Great Australian Bight, they occur in more exposed conditions to depths of -40m. *Posidonia* is not a colonizing species and only appears after the substrate has been stabilized by species such as *Amphibolis antarctica* (Labill) in Western and South Australia and *Zostera capricorni* Aschers in New South Wales. The development of *P. australis* is accompanied by the formation of a tough, wave resistant rhizome 'matte' (cf. Molinier and Picard, 1952).

Larkum (1976a) has summarized on a state-wide basis the distribution of seagrasses. Since Larkum's review, Shepherd and Womersley (1976) have described the seagrass communities around St. Francis Island in the northern Great Australian Bight. New South Wales State Fisheries are currently documenting seagrass distributions along the coast (Evans and Gibbs, in press).

Considerable gaps in distribution data occur, especially in tropical regions where many species occur. Den Hartog (1970) provides the only information on tropical seagrass communities, none of which reach the density or areal size of *Posidonia australis* in temperate waters. a map detailing the distribution and extent of Australian seagrasses is given by McComb *et al.,* 1981.

Associated with the seagrasses may be rhizophytic companion species such as *Caulerpa* and *Halimeda.* Such species occur mainly in sub-tropical or tropical communities. A film of microalgae, especially diatoms, occurs on the muddy or sandy substratum in between the seagrasses. Algae are often trapped by the seagrass and may continue to grow in the shelter of the beds (den Hartog, 1979). This associated flora has been neglected in Australia.

Primary Productivity Studies

McRoy and McMillan (1977) have suggested that such common plants as seagrasses with such a high primary production must be of immense ecological importance. Consequently, 'seagrass ecosystems' have become a popular focus for research throughout the world, including Australia. Recently, considerable advances have been made in measuring the rates of primary production of some temperate species here in Australia.

The preferred method of measuring primary productivity amongst seagrass workers seems to be measuring the production of organic matter directly, i.e. by measuring the increase in blade length. This method has the distinct advantage that it can give an integrated measure of primary productivity over a number of days. The method has drawbacks, in that it measures only the productivity of part of a plant, the frond, and it does not take into account any losses of dissolved organic carbon compounds (Larkum, 1981), which may be significant (Kirkman and Reid, 1979).

Rates of leaf blade production of *Posidonia australis* range from 0.7-5.5 g dry wt. m^{-2} day, depending on site and season. It is significantly higher in clear waters, such as Jervis Bay, than in disturbed areas like Botany Bay, New South Wales. Maximum rates occur in the middle of the geographical range of this species, which is Spencer Gulf, South Australia (West and Larkum, 1979).

Leaf production is markedly seasonal with a maximum production between November and February, and a minimum in July to August. However, if flowering

occurs in July, then leaf blade production is severely curtailed. In Botany Bay three to four crops of leaves are produced annually. In areas of frequent storms, biomass figures may be relatively constant (West and Larkum, 1979).

In some areas such as Westernport Bay, Victoria, nitrogen limits the growth of *Heterozostera tasmanica* during spring and early summer (Bulthuis and Woelkerling, 1981). This species and some other seagrasses, including *Zostera marina,* can absorb nutrients from the sediments and translocate them to the leaves (Twilley *et al.,* 1977).

Zostera capricorni shows a similar growth pattern (Larkum *et al.,* in press) which seems to be more closely related to water temperature than to solar radiation. New leaf production continues fairly uniformly throughout the year with a slight increase in the warmer months. Turnover times for leaves vary from about 33 days in the summer months to 67 days for the winter period (Kirkman *et al.,* 1982).

In Port Hacking, New South Wales, *Zostera* grows 3-4 times faster than *Posidonia australis.* As these two seagrasses occur in varying densities, comparisons of production per unit area of seagrass beds are more meaningful. *Zostera* production varies from 0.56-1.82 g m^{-2} day^{-1} while *P. australis* ranges from 0.57-1.44 g m^{-2} day^{-1} — throughout the year (Kirkman and Reid, 1979; Kirkman *et al.,* 1982).

Seagrass Faunas

STRUCTURE

The animal communities of seagrasses are considered here in four major categories:

a. infauna — animals living in the sediment associated with the rhizomes of the seagrasses,

b. epifauna — animals living on the surface of the mud at the base of the seagrass,

c. sessile communities on the blades of the seagrass and,

d. epibenthic animals, swimming in the water column between the seagrass.

SAMPLING METHODS

When designing sampling programmes the three-dimensional nature of the habitat must be considered, for each of the dimensions has an associated fauna. Seagrass communities which are exposed to air during low tide, lose one of the dimensions as the blades collapse eliminating the space between them. This dimension is restored on a rising tide. As discussed later, the fauna shows distinct diurnal, tidal and seasonal variations in composition.

The fauna can also be divided into permanent and temporary residents. Permanent residents spend their entire lives within the seagrass beds. Temporary residents spend only part of their life within the community. This element is rather heterogeneous and consists of:

1. fishes and crustaceans which spend part of their juvenile life in the beds,

2. tidal migrants, which move into the beds on a rising tide and leave on an ebb tide and terrestrial species which feed in the beds during low tide,

3. vertebrate grazers, such as ducks, turtles and dugongs.

Thus a seagrass community is in a constant state of flux as the relationship of the community and its environment change. The community can be considered as having a central core of residents whose numbers fluctuate seasonally, and migrants whose composition varies according to the time of day, tide and season.

To devise one sampling programme to study seagrass faunas is impossible. Each group of fauna necessitates a specific sampling programme, with various periodicities and intensities.

a. *Infauna*:

The dense rhizome 'matte' of seagrass beds which is well developed in *Posidonia* is the major problem to overcome in sampling infauna. Collett *et al.* (in MS) used a hand-operated corer with a good cutting edge to penetrate the 'matte;. Poiner (1980) successfully used a 0.1 m² Smith — MacIntyre grab in beds of *Halophila* and Hutchings *et al.* (1978) used a similar grab in *Zostera* and patchy *Posidonia*. This grab is not efficient in dense *Posidonia*.

Collett *et al.* (in MS) found that 15-20 samples (0.03 m²) in *Posidonia* beds in New South Wales were needed to sample 70% of the smaller infaunal species. The samples were collected from an area of visually uniformly dense beds. Hutchings *et al.* (1978) sampling *Zostera* and patchy *Posidonia* found that the number of samples required to reach the upper asymptote of the respective species-volume curve varied from 4-10 samples.

All infaunal studies should ascertain the minimum number of samples necessary to collect 70% or more of the species present. This has not been standard practice.

The most commonly used mesh size is 1 mm (Collett *et al.*, in MS; Poiner, 1980; Rainer, 1981; Rainer and Fitzhardinge, 1981). To facilitate the sorting of animals from in amongst the large amount of plant matter, add Rose Bengal to the 7% formalin solution, until a deep pink colour develops. All living, animal material becomes dark pink in colour, considerably facilitating sorting. Micro-crustaceans can be collected from the sieved fractions by running a steady stream of water over the samples. The micro-crustaceans float off the samples which are gently agitated and are retained in a sieve.

Poiner (1980) determined the density of seagrasses in the area of his infaunal samples by counting the number of nodes per 0.25 m². He also analysed the sediment using standard methods of granulometric analysis (Buchanan, 1971). Such associated data are invaluable in interpreting the benthic fauna and should become standard practice.

Lewis and Stoner (1981) have recently compared macrofaunal sampling methods in seagrass beds. Three different-sized core samples were tested for their relative efficiencies. Core samples were sieved with both 0.5 and 1.0 mm mesh screens. The smaller core was the most efficient and this was attributed to the problems of penetrating the dense root 'matte'. The 0.5 mm sieve retained approximately 50% more individuals than the 1.0 mm sieve.

For sampling larger infauna such as bivalves. *Anadara* and *Trapezia,* 0.25 m² quadrats are laid and the sediment searched within each quadrat by a diver. Hutchings and Recher (1974) used 40 such quadrats.

b. *Epifauna*:

Techniques that have been used include visual observations by divers along transects (Rainer, 1981; Shepherd, 1974) and small seines pulled through the seagrass (Hutchings and Recher, 1974). Both methods are qualitative.

No quantitative study of this community has been undertaken in Australia.

c. *Epiphytes*:

No quantitative survey has been carried out on this fauna. Hutchings and Recher (1974), while measuring density of seagrasses, scraped off the associated fauna. The polychaetes are described by Hutchings and Rainer (1979).

d. *Epibenthic*:

Young (1978) sampled with a roller beam trawl between fixed markers

fortnightly over a 12 month period. All stations were sampled within 2 days of the new and full moon. All samples were collected within 2 hours of the night high tide. The trawls were made towing into the current. Various mesh sizes were tested and optimum size for crustaceans was 2 mm for the body of the net and a cod end of 1 mm. A larger mesh size of 2.5 mm for the body of the net was used in a subsequent study (Young, 1981).

Robertson and Howard (1978) sampled the zooplankton in *Zostera* and *Heterozostera* beds, by using plankton tows of 10 minutes duration. The mesh size was 254 μm and the net had a 30 cm mouth diameter. The upper zone of the water column was sampled by maintaining the top of the net at 10 cm. The volume of water sampled was measured by a digital flow meter.

For fish, Scott (1981) used a mesh of 1.5 mm and trawls of 1-2 minutes duration covering a distance of 30-50 m. Sampling was considered sufficient when no additional species were found.

Robertson and Howard (1978) used a 30 m seine net (1 cm mesh bunt and 1.25 cm mesh wings) to catch large, fast swimming and mid-water living fish. Smaller benthic fish were obtained by using a hand laid 10 m (1 mm mesh) seine net. Samples were taken on the rising and falling tide, by day and by night. Robertson measured the bias introduced into density estimates through fish avoiding the seine net in the study area. The results indicate no apparently significant difference in the efficiency of the net in capturing the major pelagic species, but efficiency values were much lower for benthic species. Although the efficiency of capture differed, the nettings accurately reflected the relative abundance of species within each group.

DESCRIPTION OF THE FAUNA

a. INFAUNA

Infauna has been the best studied faunal component of seagrass beds probably because of the relative ease of collecting quantitative data. Even so, quantitative data are restricted to temperate beds of *Posidonia, Ruppia, Halophila* and *Zostera*.

A recent survey of *Posidonia* beds along the New South Wales coast by Collett *et al.* (in MS) has shown that a large number of benthic invertebrates occur (363 species) dominated by polychaetes, crustaceans and molluscs. A large number of species (211 or 54.5%) are restricted to one site and of these 102 (26.9%) are represented by single individuals. Only two species occur at all sites. No characteristic *Posidonia* fauna occurs. Rather, the fauna is determined by the hydrological and sediment characteristics of a particular bed. Latitudinal gradients seem unimportant. Analysis of the fauna shows that marine-dominated sites are more similar than estuarine sites. The number of species and individuals occurring at sites varied greatly as did community indices. Many of the species occurring in *Posidonia* beds also occur in *Zostera* beds or in seagrass-free sediments, in the same area.

Other seagrass communities studied quantitatively include those of Tuggerah Lakes, New South Wales (Powis and Robinson, 1980). In the lakes, *Zostera capricorni, Ruppia spiralis* and *Halophila ovalis* occur typically as discrete monospecific stands. At only one site, does a mixed community of *Zostera* and *Ruppia* occur. Powis and Robinson found that the sites could be split on the basis of sediment and associated vegetation, in terms of number of species, and individuals, diversity and characteristic species. Seagrass communities are generally more diverse than mud communities. The *Zostera* sites share some species in common, although the numerical dominance varies between sites. *Ruppia* sites have lower numbers of species than *Zostera* sites. Mixed communities of *Zostera* and *Ruppia* have the highest

number of species and diversity. *Halophila* beds are intermediate between *Ruppia* and *Zostera* in terms of number of species and diversity.

Beds of *Halophila ovalis* and *H. spinulosa* have been extensively studied in Moreton Bay by Poiner (1980). He found 137 species, of which 51% are polychaetes, 33% crustaceans (including 16% amphipods and 8% decapods) and 11% molluscs (9% of which are bivalves).

The majority of these studies have shown that a richer infauna is associated with seagrasses than with bare substrate. In Moreton Bay, one of the beds of *Halophila ovalis,* which Poiner (1980) studied, disappeared during the winter, as a result of storms and strong wave action, and reappeared during the calm, summer months. Poiner found with an increase in plant growth during the summer, diversity of the infaunal community increases significantly. The rise is due to an increase in the number of individuals rather than additional species.

Several reasons have been advanced as to why seagrass communities have richer benthic faunas than bare sediment. Seagrasses dampen the sediment water interface by stabilizing sediments, baffling currents and damping wave action (Zieman, 1972; Orth, 1977). This stabilizing effect of seagrasses could allow increased settlement of larvae, prevent adults or juveniles from resuspension and reduce disruptive disturbances by, for instance, nektonic predators, surface scavengers and wave action (Poiner, 1980). Orth (1977) reported the impact of the blue crab *(Callinectes sapidus)* on the infauna of seagrasses. Powis and Robinson (1980) suggest that seagrass beds may provide a habitat of high structural complexity which, according to MacArthur (1965), would have a high species diversity (Heck and Wetstone, 1977).

However, the abundance of infauna seems to vary according to the type of seagrass. Powis and Robinson (1980), as already mentioned, found that *Zostera capricorni* has a richer fauna than either *Halophila* or *Ruppia*. Hutchings and Recher (1974) sampled the infauna of *Posidonia australis* and *Z. capricorni* and found that *Zostera* supports a more diverse community, both in terms of number of individuals and species than *Posidonia*. Powis and Robinson suggest that the well-developed 'matte' of *Posidonia* restricts the development of an infaunal community. By contrast, some of the *Posidonia* beds sampled by Collett *et al.* (in MS) yielded large numbers of individuals and species (e.g., Towra Point yielded 148 species with 4,480 individuals per m²). Powis and Robinson (1980) further suggest that the differences in infaunal diversity of different seagrasses may be related to the efficiency of individual species in binding sediment. They suggest that *Zostera* is more efficient than *Ruppia*. Orth (1977) also stresses the stabilizing properties of *Zostera marina*. Stable substrates according to Sanders (1969) can support communities of high diversity. *Ruppia,* with its poor root system and small blades, is not as efficient as *Zostera* in either of these roles and hence has lower diversity communities. Powis and Robinson do not speculate on *Halophila* beds which have intermediate values of diversity. This species does not form dense beds in Tuggerah Lakes.

There is some contradiction in the literature, regarding the endemicity of seagrass faunas. Kikuchi and Pérès (1976) developed the concept of parallelism which suggests that seagrass beds share many species in common or a 'species' is replaced by a closely related equivalent in a different geographical locality. They give several examples from the epifauna of *Zostera* beds in Japanese waters and imply it would be valid for infauna. The data from *Posidonia* beds along the New South Wales coast do not support this concept. For Collett *et al.* (in MS) were not able to define a characteristic fauna. Each site has a unique assemblage of species. Powis and Robinson (1980), similarly, did not record any species totally restricted to a particular species of seagrass in Tuggerah Lakes. Also, in Careel Bay many species occurring in

TABLE 1

Species of Polychaetes recorded from nine *Zostera capricorni* beds in N.S.W.

	Merimbula	Towra Point	Weeney Bay	Bonnet Bay	Careel Bay	Tuggerah Lakes	Lower Myall River	Wallis Lake	Wollomba River	Number of sites
Harmothoe praeclara					X					1
Parahalosydna chrysostichtus					X					1
Paralepidonotus ampulliferus		X	X					X		3
Sigalion ovigerum	X									1
Sthenelais boa								X		1
Eumida sanguinea					X					1
Gyptis sp.			X							1
Phyllodoce novaehollandiae		X	X		X					3
Sphaerosyllis sublaevis					X					1
S. nr. *semiverrucosa*					X					1
Typosyllis variegata					X					1
Australonereis ehlersi	X	X	X		X	X	X		X	7
Ceratonereis erythraeensis *	X		X	X	X		X		X	6
C. mirabilis		X	X		X	X		X		5
Platynereis dumerilii antipoda					X					1
Nephtys australiensis	X	X	X	X	X	X	X	X		8
Glycera americana		X	X		X		X			4
Marphysa sanguinea				X	X	X	X	X	X	6
Lumbrineris latreilli	X	X	X		X		X			5
Leitoscoloplos bifurcatus					X					1
L. normalis					X					1
Naineris grubei australis					X					1
Phylo felix		X			X					2
Polydora socialis					X					1
Prionospio malmgreni								X		1
Pseudopolydora kempi					X					1
Magelona dakini					X					1
Chaetopterus variopedatus					X					1
Cirriformia filigera	X									1
C. tentaculata	X									1
Hyboscolex longiseta								X		1
Armandia intermedia		X	X		X	X	X			5
Polyophthalmus pictus					X					1
Barantolla lepte	X	X	X		X	X		X		6
Mediomastus californiensis		X	X							2
Notomastus torquatus		X	X		X		X	X	X	6
Scyphoproctus djiboutiensis								X		1
Arenicola bombayensis					X					1
Owenia fusiformis	X	X	X		X	X				5
Amphicteis dalmatica					X					1
Lysilla apheles								X		1
L. pacifica		X	X		X		X	X		5
Rhinothelepus lobatus			X		X			X		3

TABLE 1 (continued)

Species of Polychaetes recorded from nine *Zostera capricorni* beds in N.S.W.

	Merimbula	Towra Point	Weeney Bay	Bonnet Bay	Careel Bay	Tuggerah Lakes	Lower Myall River	Wallis Lake	Wollomba River	Number of sites
						Sites				
Streblosoma acymatum					X					1
Pista typha	X				X					2
Amphiglena pacifica					X					1
Janua (D.) foraminosa					X					1
J. (D.) brasiliensis					X					1
Total number of species	10	14	16	3	37	7	9	13	4	

Sources of Data:
Careel Bay — Hutchings and Recher (1974) and Hutchings and Rainer (1979)
Towra Point and Weeney Bay — ALS (1978)
Wallis Lake — Hutchings *et al.* (1978)
Lower Myall River —Weate (1975) ; Atkinson *et al.* (1981)
Wollomba River — Day (1975)
Bonnet Bay — Branagan *et al.* (1976)
Tuggerah Lakes — Powis and Robinson (1980)
Merimbula — Hutchings and Murray (in prep.)

*See footnote p. 190.

the *Zostera* beds also occur in *Posidonia* (Hutchings and Recher, 1974). No characteristic species are associated with the *Zostera muelleri* and *Heterozostera tasmanica* communities in Westernport Bay, Victoria (Littlejohn *et al.*, 1974). Similarly, the *Zostera* communities in Gippsland Lakes (Poore *et al.*, 1977) lack characteristic species. However, Poiner (1980) found 35 species restricted to beds of *Halophila ovalis* and *H. spinulosa* but does not list them.

Even if the concept of Kikuchi and Pérès (1976) is rejected, there is evidence that similar trophic levels operate within seagrass communities. Collett *et al.* (in MS) found that the very different faunal communities in the *Posidonia* beds are all dominated by detritus feeders, either feeding on detritus within the sediment (deposit feeders) or in suspension (filter feeders). Similarly, the infauna of *Zostera muelleri* and *Heterozostera tasmanica* in Westernport Bay, Victoria (Littlejohn *et al.*, 1974) are dominated by detritus feeders. Of the 44 species present, 14 are selective deposit feeders, 10 are non-selective deposit feeders and 3 are filter feeders. Polychaetes represented 50% of the biovolume.

As polychaetes are often the dominant group of animals in the infauna, I have extracted from the literature species occurring in *Zostera* in New South Wales. Many of these studies were carried out by myself or else I confirmed the identifications so that consistent names have been given to the species (for several of these species pose taxonomic problems). The sites in Table 1 have been arranged latitudinally. *Zostera capricorni* flourishes in a variety of salinities, from almost fully marine, as in Careel Bay, to upper estuarine areas such as Wollumba River which flows into Wallis Lake or Bonnet Bay on the Woronora River, where considerable fluctuations in salinity occur. Fully marine sites such as Careel Bay have the richest polychaete fauna (37 species) and upper estuarine areas such as Bonnet Bay and Wollumba River have relatively few species (3 and 4, respectively) which may be abundant, however. Such data reinforce the concept that although seagrasses provide some benefits in stabilizing sediment, factors such as salinity regimes have an overriding effect on the faunal community. The polychaete fauna varies considerably between sites, and 30 species (62.5%) occur at one site only; no species is shared by all 9 sites. However, certain families of polychaetes are commonly present in infaunal communities, for example, all sites possess at least one species of nereid (*Australonereis ehlersi*, *Ceratonereis erythraeensis**, *C. mirabilis* or *Platynereis dumerilii antipoda*) and all sites except Bonnet Bay have at least one species of capitellid (*Barantolla lepte, Mediomastus californiensis, Notomastus torquatus, Scyphoproctus djiboutiensis*). These two families are well represented in other seagrass beds (Collett *et al.*, in MS) and Hutchings and Turvey (in MS) have collected 10 species of nereids from seagrass beds in South Australia. Capitellids are non-selective deposit feeders. Nereids are often assumed to be carnivores, as they have well developed jaws but are probably scavengers or omnivores.

Fluctuations in seagrass infaunal communities

i. Seasonality

Seagrass beds exhibit strong seasonality of growth, maximum growth occurs during the spring and summer. In the autumn and winter, much of this growth dies and is broken off and may be washed out of the seagrass beds. Severe storms may cause loss of seagrass leaves, and even rip out the seagrass 'matte'.

Ceratonereis erythraeensis is a complex of species currently being described by Hutchings and Turvey (in MS). *Ceratonereis erythraeensis* Fauvel probably does not occur in Australia.

Hutchings and Recher (1974) recorded strong seasonality of infauna in both *Posidonia* and *Zostera* beds. Both showed fluctuations in the number of species, with maximum numbers occurring in June. Numbers of individuals also fluctuated with maximum numbers in November in *Zostera* beds and in June in *Posidonia*.

Mass settlement of some species occurs. Two polychaetes *Scoloplos* (*S.*) *simplex* (originally referred to as *Haploscoloplos* n. sp.) and *Ceratonereis erythraeensis* (originally referred to as *Nereis diversicolor* but see footnote here) settle in large numbers between June and November and, similarly, the mollusc *Macoma deltoidalis*. Many species occur sporadically in the seagrass beds (Hutchings and Recher, 1974).

Poiner (1980), working on *Halophila* communities, measured the community flux at 2-monthly intervals. Community flux is a measure of the degree to which species contributions within a particular site (measured as weighted change in abundances of individual species) are exchanged or given up altogether between sampling periods. The community flux is low for permanent beds of *Halophila*, whereas the flux in beds showing marked seasonal changes, fluctuate widely. In these beds the number of species remains relatively constant, but an increase in the number of individuals is strongly correlated with an increase in the density of *Halophila*.

ii. Flooding

Severe floods occurred in Tuggerah Lakes while Powis and Robinson (1980) were sampling the infauna. *Halophila* beds were severely reduced. Associated with the rain was a severe storm with strong winds. This resulted in the devastation of some beds of *Zostera* and *Ruppia*. After the floods limited re-establishment of fauna in muddy areas occurred; this did not happen in the seagrass areas. Powis and Robinson suggest that the loss of *Halophila* roots, resulted in a decrease in habitat availability.

In the lower Myall River and Myall Lakes, New South Wales, widespread destruction of *Zostera* occurs periodically, probably as a result of salinity reductions. The effect on the associated benthic faunas has not been substantiated (Atkinson *et al.*, 1981).

b. EPIFAUNA

No quantitative data are available on this community. Qualitative studies have been carried out in Cockburn Sound, Western Australia. Echinoderms (Marsh and Devaney, 1978), and molluscs (Wells, 1978, and Wilson *et al.*, 1978) were identified. With the demise of seagrass beds (Cambridge, 1979) one of the echinoids *Temnopleurus michaelseni* is also declining in numbers. This species was abundant in the early 70s. Similar studies have been carried out in the upper Spencer Gulf of South Australia by Shepherd (1974). He found an inverse correlation between the density of *Posidonia* and the abundance of filter-feeding molluscs, *Pinna*, *Malleus* and *Trichomya*, the sea urchin *Heliocidaris* and the ascidian *Polycarpa*.

Water movement under the seagrass canopy is about 30% of that above the canopy. This may explain the relatively small numbers of filter-feeding organisms occurring in dense seagrass beds.

The bivalve *Anadara trapezia* recruits successfully only periodically so that within a seagrass bed one age or size class dominates (Hutchings and Recher, 1974; Dixon, pers. comm.). Since 1974, there has not been a successful recruitment to Careel Bay, New South Wales, and widespread mortality (perhaps naturally as the population ages) is currently occurring (Recher, pers. comm.).

c. SESSILE COMMUNITIES ON THE BLADES OF THE SEAGRASSES

The epiphytic fauna of Australian seagrass beds has not been studied as a separate component.

Anink (1980) reports that the number of epifaunal species so far observed is far fewer than the number reported settling on artificial substrates.

d. EPIBENTHIC COMMUNITIES

Young (1978) has extensively studied the distribution of one component of epibenthic communities, namely prawns in Moreton Bay, Queensland. Four species of penaeid prawn were studied in detail. They utilize all available littoral areas in the bay, only some of which contain seagrasses. The distribution of prawns differs but is related to the prevailing salinity and temperature regime and the seagrasses.

The maximum abundances of post-larvae of all four species occur within two seagrass communities (*Zostera capricorni* and *Halophila ovalis* or *Z. capricorni*, *Halodule uninervis* and *H. ovalis*). Three of the four species show increase in abundances in summer which coincides with the increased abundance of *Z. capricorni* and *H. ovalis*. However, the other species has reduced numbers at this time suggesting no simple relationships. Young was unable to isolate or attribute the relative importance of these individual factors.

A similar complex pattern exists among the entire epibenthic community (Young and Wadley, 1979). The type of sediment and the presence of seagrasses are again important but the major factor is salinity. Salinity regimes are major determinants in seagrass distribution, but depth is also important (Young and Kirkman, 1975). Young and Wadley (1979) were unable to quantify the importance of specific seagrass beds in determining their associated epibenthic fauna.

In a subsequent study, Young (1981) attempted to eliminate some of these variables. He selected two adjacent beds of *Posidonia australis* and *Zostera capricorni*, in similar depths of water in Port Hacking, New South Wales. Significant differences in the species composition and abundances of the epibenthic fauna occur, with *Posidonia* being the richer community. Young suggests that the differences in the fauna of the two seagrasses are controlled by external events leading to variable recruitment success, although he also suggests that the resources offered by the seagrasses present a habitat which many species recognize and utilize. Wadley (1981), working in the same area, showed that temporal heterogeneity of the epibenthos, although significant, is small compared with spatial heterogeneity. Differences in the fauna associated with the month and season of sampling show strong interaction with the type of habitat. The absence of change in the major components of the fauna during flood and the overall temporal homogeneity in samples indicate relatively stable communities despite the unpredictable environment. Young (1981) further suggests that the more diverse community of *Posidonia australis* is not significantly more stable than the *Zostera* community. This greater diversity of epibenthic fauna is the reverse of infaunal communities, where the *Zostera* is more diverse (Hutchings and Recher, 1974).

Fish

Relatively few studies have been carried out on the fish communities of seagrass beds. Scott (1981) sampled the fish fauna of *Posidonia* beds in Geographe Bay, Western Australia. Nineteen species occur, and the most abundant species is the odacid *Neoodax radiatus* (weed whiting).

Hoese (1978, pers. comm.) has studied the fish communities occurring in seagrass beds in coastal lagoons in New South Wales. These lagoons are periodically closed to the sea. The communities fluctuate both in terms of number of individuals and species. Recruitment appears to be solely from the sea, when the lagoons are open, rather than from other parts of the lagoon. This is in contrast to Scott's (1981) study where the fish complete their life cycle within the seagrass.

Other fish studies by Bell *et al.* (1978a, b), Conacher *et al.* (1979) and Littlejohn *et al.* (1974) have been related to investigating the feeding patterns of the fish. This will be discussed in the energy flow section.

Zooplankton

Holoplanktonic calanoid copepods and meroplanktonic decapod larvae are numerically dominant in the water column during the day in *Zostera* beds in Westernport Bay, Victoria (Robertson and Howard, 1978). However, the number of such animals is significantly lower than that collected at night. This pattern of low catches near the surface during the day and high numbers at night has been recorded on a number of previous occasions (Howard, unpublished data). These obligate planktons have also been taken in planktonic trawls made close to the substrate during the day. Thus estimates of zooplankton samples taken near the surface underestimate the true density of these organisms throughout the whole water column during a 24-hour period.

Amphipods are benthic during the day, at night they form a conspicuous component of the plankton.

Ostracods, which are infaunal by day also enter the water column at night but at lower densities than amphipods.

Energy Flows within the Seagrass Communities

Kirkman and Reid (1979) have constructed a carbon budget for *Posidonia australis* in Port Hacking, near Sydney. They measured biomass, calculated grazing rates by herbivores, estimated the amount of floating seagrass detached from the beds and collected the sinking *Posidonia* detritus below the seagrass beds.

Small seasonal variations in biomass occur. Three species of Monacanthidae (leatherjackets), *Monacanthus chinensis, Meuchenia freycineti* and *M. trachylepsis* consume large amounts of *Posidonia*. Bell *et al.* (1978b) calculated that adult *M. chinensis* have a diet consisting of 41.7% *P. australis* by estimated volume. However, looking at the entire *Posidonia* beds, herbivores do not consume an appreciable amount of attached *Posidonia* (Conacher *et al.*, 1979).

The amount of floating *Posidonia* is related to winds and, unlike *Zostera,* is not washed up onto beaches in New South Wales. However, in South Australia large beds accumulate on beaches adjacent to seagrass beds. *Posidonia* occurs typically in greater depths than *Zostera.* Leaves that are added to the organic detrital cover of sediments make up the majority of particulate organic C lost from the seagrass beds. Only heavily epiphytized leaves sink. Between 27-71% of the biomass collected in the traps is epibiota.

Dissolved organic carbon accounted for the greatest loss of organic C from the system.

A less extensive study of the *Zostera* beds in Port Hacking by Kirkman *et al.* (1982) has shown that the growth of *Zostera* is 3-4 times that of *Posidonia* in the same

environment. The production figures are for *Zostera* 0.56-1.82 g m⁻² day⁻¹ while *P. australis* shows a production rate of 0.57-1.44 g m⁻² day⁻¹ through the year.

It seems likely that a similar breakdown of the C budget occurs in *Zostera* beds as Kirkman and Reid (1979) have described for *Posidonia* in the same environment.

Larkum (1981) has estimated the percentage contribution of each of the primary producers in the estuarine ecosystem of Botany Bay. Although seagrass beds do not occur as extensive beds, they contribute 25% to the total budget of the bay. This percentage includes the contribution made by the epiphytic algae which occur on the seagrass blades.

Assuming that Kirkman and Reid's (1979) data from Port Hacking are of general applicability, the important contribution of seagrasses to the estuarine ecosystem is the continual supply of leaves to the organic detrital cover of the sediments. Attiwill and Clough (1974) have also stressed the importance of this production of organic matter by the seagrass beds in Westernport Bay, Victoria.

Little work has been done on the breakdown or shredding of this continual supply of leaves. Brand (1977) has experimentally investigated the production of detritus from the breakdown of *Zostera* by the amphipods *Parhyalella* spp. This was to quantify part of the model of the C budget proposed by Brand *et al.* (1974) for estuarine ecosystems. The amphipods ingest the epiphytes on the blades of the *Zostera*. Brand does not provide any evidence that the amphipods actually obtain nutrients from the plant matter but implies that nutrition is obtained mainly from the attached biota. The amphipods produce nitrogen-enriched faecal pellets which facilitate further breakdown of the *Zostera* fragments. Seagrass leaf tissue is extremely refractile (Godshalk and Wetzel, 1978) and the decay of the structural carbohydrates may be the rate limiting step in the transfer of energy through seagrass ecosystems (Harrison and Mann, 1975). Animals which can utilize these fragments appear to be mainly amphipods (Robertson and Mann, 1980), although some herbivorous polychaetes may be involved. Overseas, attempts have been made to trace the origin of detritus in the diets of estuarine animals by measuring the ratio of ¹³C:¹²C. These ratios differ sufficiently in seagrasses and phytoplankton to allow the source of the detritus to be traced (Fry and Parker, 1979; McConnaughey and McRoy, 1979; Thayer *et al.*, 1978). As mentioned earlier, few fish of seagrass beds in Australia are herbivores. The leatherjackets do obtain some nutrients from ingested *P. australis* fragments (Conacher *et al.*, 1979). Most of the fish occurring in seagrass are carnivores (Littlejohn *et al.*, 1974; Scott, 1981) feeding on the detritus-feeding crabs, molluscs and polychaetes (Robertson, 1980). Although Robertson and Howard (1978) have documented the importance of zooplankton for several fish species, fish diets may shift during the year as prey species fluctuate (Littlejohn *et al.*, 1974).

The importance of detritus feeders (Tenore, 1977) which dominate the benthos is related to the further breakdown of the plant matter by mechanical abrasion as it passes through the guts of the detritus feeders (Fenchel, 1970, 1977). This increases the surface area to volume ratio, and hence the bacterial and algal populations on the particles (Newell, 1965). Many of these detritus feeders are probably obtaining nutrients from the associated flora and fauna rather than from the seagrasses. During the production of detritus some organic compounds are produced which can be taken up directly by the seagrasses themselves (Bulthuis and Woelkerling, 1981) so that a close relationship between the infauna and seagrasses occurs.

Where they occur, vertebrate grazers of seagrass beds may have considerable local impact on the beds. *Dugong dugon,* a marine mammal, occurs in large herds in coastal waters of northern Australia. The dugong feeds exclusively on seagrasses (Heinsohn and Birch, 1972). In the Townsville region they feed selectively on

Diplanthera and *Cymodoce.* Two other common seagrass species in the region, *Enhalus acoroides* (L.f.) Royle and *Syringodium isoetifolium,* are not eaten. Dugongs eat the entire plant (leaves, rhizomes and roots), and ingest some animals and algae.

They graze most heavily in beds of low density (biomass 10-30 g dry matter/m²), producing trails of a depth of 3-5 cm. They remove on average 63% of the seagrass from the trails with a maximum of 86% (Heinsohn *et al.,* 1977). Two captive dugongs ate 50-55 kg of seagrass per day (equivalent to 2 tonnes dry weight/annum) (Jones, 1967). During feeding some seagrass is damaged although not ingested. Assuming a grazing efficiency of 63% and a seagrass community biomass of 94 kg dry matter/m² (Heinsohn, unpublished data from Cleveland Bay, Townsville) 3.5 ha is required to support a dugong for a year. The area over which dugongs graze is not known but should be if the impact of their grazing on seagrass beds is to be assessed.

Turtles also feed on seagrasses, but not exclusively. The green turtle *Chelonia mydas* feeds on marine algae and seagrasses, including species of *Zostera, Enhalus, Thallassina, Posidonia* and *Halodule.* Loggerhead turtles *Caretta caretta,* also eat seagrasses, but are primarily carnivores. Similarly, Hawksbill turtles *Eretmochelys imbricata,* eat seagrasses but mainly as juveniles (Rebel, 1974).

Wading birds are important temporary residents during low tide. Water fowl such as black swans, *Cygnus atratus,* are estimated to eat 230 tonnes of *Ruppia* and the freshwater *Potamogeton* a year in the Blackwood River estuary in Western Australia (Hodgkin, 1978). Delroy (1974) calculated that 90% of food of black ducks (*Anas supercil*), musk duck (*Biziura lobata*) and grey teal (*Anas gibberifrons*) consisted of tubers and seeds of *Ruppia* and *Lamprothaminium* in the Coorong, South Australia. They feed by pulling plants to the surface, thus damaging more than they eat. They feed only during the summer on seagrases in this estuary. Ferguson Wood (1959) suggested that black swans caused great damage to *Zostera capricorni* beds.

Seagrass beds are also used by a variety of water birds including pelicans (*Pelecanus conspicillatus*), cormorants, etc. Pelicans and cormorants feed on schooling fish within the seagrass beds. For birds such as herons (Ardeidae) which stalk their prey, the presence or absence of seagrass beds probably determines the number of individuals in an area. In dense seagrass beds, water clarity is improved, more sedentary fish are present, giving herons ample opportunity to feed during low tide. In areas of sparse or no beds, the water is more turbid, fewer sedentary species of fish are present and herons must expend far more energy in catching fish. Such areas will have fewer herons than areas with dense seagrass beds. Recher (pers. comm.) points out that although herons and egrets are predominantly fish eaters, in marine habitats crustaceans are an important part of their diet.

Migrant waders, are less dependent on seagrass beds. They are limited to low tide and will often feed in non-grass situations. They feed on molluscs, annelids and crustaceans, although a particular species may be highly selective. For example, the knot feeds on surface-living molluscs whereas the bartailed godwit *Limosa lapponica* feeds preferentially on polychaetes and the eastern curlew *Numenius madagascariensis* on *Callianassa* sp. (Recher, pers. comm.).

DISCUSSION

Concluding this review, I would like to consider the direction of future studies of seagrass communities. Recent trends in ecological studies of these communities overseas have been to manipulate the system experimentally.

Orth (1977) has been able to quantify the importance of seagrass beds in

stabilizing sediments and the production of organic material by artificially removing *Zostera*. He could then compare intact *Zostera* with clipped beds. Such methods could be extended to quantify the relative importance of different species of seagrasses in Australia.

Other experiments have tested the hypothesis that seagrass provides shelter from predation, by caging experiments (Heck and Thoman, 1981). Such information is essential if the much-quoted statement that seagrasses act as nursery grounds and provide shelter and protection is to be substantiated. How do different seagrasses compare? Are some species more efficient than others? Young and Young (1978) have experimentally investigated the factors important in regulating species densities and diversities in seagrass associated benthos.

Such studies urgently need to be conducted here in Australia for this experimental approach seems to be a productive way of determining the factors important in maintenance of seagrass communities. Unless we know these factors, the management of seagrass communities cannot be soundly based. We also need more integrated studies like those of Kirkman and Reid (1979) but these should be extended to include the faunal components. Rates of turn-over of the dominant animals must be determined.

The data from Australian seagrass communities clearly show the importance of seagrasses. Some of the primary productivity studies indicate the variations between sites (Larkum, 1981). Are similar fluctuations occurring in the animal communities? Larkum (1981) has suggested that these variations are sometimes caused by urban stress. Unless we understand the entire community we will not recognize the early symptoms of a community under stress, and thus be able to take remedial action. Loss of seagrasses will have serious impacts on the fishing, oyster and prawning industries (AMSA, 1977; Young, 1978).

Oil spills and the use of oil dispersants and other types of industrial pollution severely affect the growth of seagrass beds (Larkum, 1976b) and hence affect the associated fauna (Jacobs, 1980). The number of oil spills and incidents of industrial pollution are increasing and unless checked will have major effects on the seagrass ecosystems and subsequently on estuarine and shallow coastal ecosystems.

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